SHORT COMMUNICATION

WATER SURFACE LOCOMOTION BY SPIDERS: DISTINCT GAITS IN DIVERSE FAMILIES

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ABSTRACT.   Pisaurids such as *Dolomedes triton* (Walckenaer 1837) are well known as inhabitants of ponds and streams and are adept at locomotion on the water surface. In a broad survey of water surface locomotion in spiders, we have found that most taxa do not use specialized gaits under these circumstances. However, some tetragnathids, araneids, and salticids (three families that are outside of the superfamily Lycosoidea to which the pisaurids belong) resemble *D. triton* to the extent that they do use specialized gaits when on the water surface. Of these, the tetragnathids are particularly accomplished at water surface locomotion, achieving velocities that exceed those of *D. triton* when it rows, but not when it gallops.

Keywords: Aquatic locomotion, gaits, Pisauridae, Tetragnathidae, Philodromidae, Salticidae, Araneidae, Lycosidae, Gnaphosidae

Spiders in the family Pisauridae typically frequent the edges of bodies of water and many of them rely on the water surface for foraging, escape from predators, and the detection and pursuit of mates. For these spiders, the perception of being on the surface of water elicits either a rowing gait or a galloping gait (Shultz 1987; Barnes & Barth 1991), the former used exclusively on water and under conditions that do not require rapid locomotion, and the latter used when speed is required. The natural contexts in which pisaurids use these gaits (McAlister 1959; Shultz 1987; Gorb & Barth 1994; Suter & Gruenwald 2000a, b) and their biomechanical properties (Suter et al. 1997; Suter & Wildman 1999) suggest that the ancestors of the pisaurids succeeded in part because of the efficacy of these specialized gaits. A number of other spider families also have representatives that frequent the edges of ponds and streams (e.g., Tetragnathidae) and still others, while strongly terrestrial in habit, must contend with periodic flooding (e.g., gnaphosids).

In the context of a broad study of the occurrence of pisaurid-like aquatic locomotion in the Araneae, we have noticed (a) that several families outside of the Lycosoidea (which includes the Pisauridae) contain members that exhibit a specialized aquatic gait different from that used by pisaurids, and (b) that

in some taxa the walking gait characteristic of most terrestrial spiders on land can work very well on the water surface. In what follows, we describe the specialized gaits of *Tetragnatha* spp. Latreille 1804 (Araneae, Tetragnathidae), *Dolomedes triton* (Walckenaer 1837) (Araneae, Pisauridae), two jumping spiders, *Habronattus hallani* (Richman 1973) and *Phidippus* sp.C.L. Koch 1846 (Araneae, Salticidae), two orb-weavers, *Neoscona* sp. Simon 1864 and *Larinioides* sp. Caporiacco 1934 (Araneae, Araneidae), and *Tibellus* sp. Simon 1875 (Araneae, Philodromidae). We follow those descriptions with an analysis of the efficacy of the gaits in contrast to the walking gaits used on water by *Geolycosa rogersi* Wallace 1942 (Araneae, Lycosidae) and *Herpyllus ecclesiasticus* Hentz 1832 (Araneae, Gnaphosidae). Voucher specimens are deposited in the Mississippi Entomological Museum at Mississippi State University, Starkville, Mississippi.

We studied the locomotion of the spiders by releasing each into a glass or plastic arena with a floor area of approximately 0.16 m² covered to a depth of at least 2 cm with water (tap water whenever distilled water was unavailable; surface tension differences between distilled and tap water are negligible in this context). Video images of the movements of each spider, captured from directly above

Table 1.—Gaits used in locomotion across the water surface. When a specialized gait is not employed all of the time, the usual alternative in each case is a gait resembling walking and thus scored as 0 0 0 0 (see text for explanation of scoring). Video clips of the aquatic locomotion of *D. triton*, *Tetragnatha* spp., a salticid, and *G. rogersi*, can be viewed at the following website: http://faculty.vassar.edu/suter/comparisons/. *For *Tibellus*, we are skeptical that this constitutes a gait specialized for aquatic locomotion (see text).

Taxon	Specialized aquatic gait	Leg-pair score	Incidence of specialized gait
D. triton Pisauridae	Legs I and IV held motionless; legs III and II, in that order, provide rowing propulsion, members of each pair sweeping in unison	1 1 1 1	Always
Tetragnatha spp. Tetragnathidae	Legs I sweep out and to the side, alternating, and provide propulsion; legs II, III, and IV move in alternation	0 0 0 0	Always
Tibellus sp. Philodromidae	Legs I, III, and IV move in alternation; legs II sweep out and to the side, in unison, but appear not to provide more propulsive power than do the other legs	0 1 0 0	Always*
Pooled salticids Salticidae	Legs III, in unison, sweep out and to the side, providing rowing propulsion; legs I and II also sweep, but with little power; legs IV trail behind	1 1 1 1	Occasional
Pooled araneids Araneidae	Legs II and I, in that order, provide rowing propulsion, members of each pair sweeping in unison; legs III also sweep in unison, but with little power; legs IV trail behind	1 1 1 1	Rare
G. rogersi Lycosidae	(terrestrial walking)	0 0 0 0	Never
H. ecclesiasticus Gnaphosidae	(terrestrial walking)	0 0 0 0	Never

the arena, were digitized at 250 frames/sec by a high-speed motion analysis system (MotionScope S series, Redlake Imaging Corporation) and then recorded in VHS format at 30 frames/sec (JVC HR-S5400U). The movements of the spiders, slowed to about 1/8 the natural speed, could be qualitatively analyzed on a video monitor. We performed more detailed measurements (e.g., of absolute velocity) via frame-by-frame analysis in NIH Image, an image analysis shareware product available from the National Institutes of Health (http://rsb.info.nih.gov/nih-image/). Detailed descriptions of the measurement method have been published elsewhere (Suter et al. 1997; Suter & Wildman 1999).

In our qualitative analyses, we considered the following: for each pair of legs, did the members of the pair move in unison or alternately, or were the legs held motionless relative to the body of the spider? In our analyses of velocity, we used the linear measurement tools in NIH Image to determine the distance traveled over several strides during relatively straight-line locomotion, and divided that distance by the elapsed time as shown in ms on the recorded high-speed images.

The rowing gait of *D. triton*, with which we were already familiar from earlier studies (e.g., Suter et al. 1997; Suter & Wildman 1999), can be charac-

terized as involving pair-wise rowing motions by legs III and II, in that order, while legs I and IV are held approximately motionless in front of and behind the spider, respectively. In contrast, when *D. triton* walks on land, it employs an alternating tetrapod gait (Barnes & Barth 1991; Shultz 1987) in which the members of a leg pair move alternately and all eight legs are involved in propulsion. When *D. triton* gallops across the water surface, only legs IV remain relatively motionless while the three anterior pairs of legs stroke approximately in unison. Thus in both of *D. triton*'s aquatic gaits, legs I are non-alternating (they are either still or move in unison), legs II and III move in unison, and legs IV are non-alternating. We found it useful in visualizing these gaits and in comparing other gaits to them, to assign the value 1 to a pair of legs if the members of the pair moved in unison or were still, and the value 0 to a pair of legs that moved alternately. Using that set of rules, both rowing and galloping by *D. triton* are scored as 1 1 1 1, whereas walking on land by the same animal is scored as 0 0 0 0.

Table 1 provides not only brief descriptions of the aquatic gaits employed by the species in this study but also leg-pair scores for these gaits. Note that the scores shown in the table ignore variability

within and between individuals because the purpose of the scores in this paper is to provide a shorthand characterization of specialized aquatic gaits rather than to evaluate the frequency with which they are used. A detailed analysis of gait variability will appear elsewhere (Stratton et al. in preparation). We have included in the table a column to provide a qualitative estimate of the incidence of each specialized gait. Video clips of the aquatic locomotion of representative taxa used in this study can be viewed at the following website: http://faculty. vassar.edu/suter/comparisons/.

We considered a gait to be specialized for aquatic locomotion if (a) it differed qualitatively from the gait used on land and (b) we could detect in the motions of the spider evidence that the novel leg motion produced thrust. On land, for example, *Tetragnatha* spp. move rather awkwardly, propelling forward in the alternating tetrapod gait that characterizes the locomotion of most spiders on solid substrates (Barnes & Barth, 1991; Shultz, 1987). On the water surface, the spider uses its legs in the same sequence (the members of each contralateral pair of legs alternating), but the locomotion is dominated by the alternating backward sweeps of the two anterior legs. Their motion is in the plane of the water surface (on land, their motion is in a plane nearly perpendicular to the substrate) and causes a pronounced, rhythmic "wag" in the animal's elongate body as the spider surges forward with the stroke of each leg. Thus the gait is qualitatively different from what is used on land and the sweep of each anterior leg causes a noticeable change in the motion of the spider (in this case, both a wag and a surge forward).

Criteria (a) and (b) were met by *Dolomedes triton*, *Tetragnatha* spp., by the salticids and by both species of araneids used in this study (note that many of the salticids and araneids we tested in the broad survey did not adopt qualitatively different gaits than those used on land). Among these, *Tetragnatha* spp. stands out because their aquatic gait involves legs in alternation, whereas the aquatic gaits of the others all involve propulsion by contralateral legs stroking in synchrony (Table 1).

In contrast, three of the species in this study, *Tibellus* sp., *G. rogersi* and *H. ecclesiasticus*, have only one gait on the water surface, and it is the same walking gait that these spiders use on land. Thus, criterion (a) was not met by these spiders. In this respect, *Tibellus* is particularly interesting because its aquatic gait resembles rowing with legs II. On the water surface, this spider walks with six legs (I, III, IV) in the alternating hexapod gait that characterizes land locomotion by insects. Legs II are longer and are held out to the sides, appearing to stroke backwards in unison. But their strokes do not result in surges in the forward motion of the spider, nor is there any other evidence that the movements

of these legs affect aquatic locomotion (c.f., criterion b). We studied videotapes of *Tibellus*'s locomotion on land and observed precisely the same pattern of leg motion (c.f., criterion a). We have tentatively concluded that, for this spider, legs II are used as antennae, monitoring the environment as it passes by to either side. Certainly we see no evidence that these legs function in propulsion on the water surface.

Absolute and relative velocities give some indication of the efficacy of locomotion, that is, how well it works. For the spiders in this study mean velocities ranged between 0.019 ± 0.010 m/s (mean $\pm$ S.E.) and 0.172 ± 0.015 m/s (Fig. 1), and relative velocities ranged between 2.74 ± 1.26 body lengths per second and 29.13 ± 2.58 bl/s (Fig. 2). A parametric ANOVA on the absolute velocity data revealed significant ($P = 0.0001$) between-taxa variation. Post-hoc tests (Fisher's PLSD) showed that *Tetragnatha* spp was significantly faster ($P < 0.05$) than each of the other taxa except *Tibellus* sp., and that *D. triton* was significantly faster ($P < 0.05$) than the salticids, the araneids, *G. rogersi* and *H. ecclesiasticus*. There were no significant absolute velocity differences among the five taxa excluding *Dolomedes* and *Tetragnatha*.

An ANOVA on the relative velocity data revealed significant ($P = 0.0001$) between-taxa variation. Post-hoc tests showed that *Tetragnatha* spp. was significantly faster ($P < 0.05$) than each of the other taxa, and that there were no other significant relative velocity differences.

Our assumption at the start of our investigation was that spiders such as *Tibellus* sp., *G. rogersi* and *H. ecclesiasticus*, which have the same walking gait on land and on the water, would underachieve when their aquatic locomotion was compared to that of spiders with specialized gaits. Why, otherwise, would specialized gaits have evolved? That rationale for the presence of specialized gaits is supported by our data on *Tetragnatha* spp. and *D. triton*, both of which perform significantly better in terms of absolute velocity than do the two non-specialists on which we have adequate data (*Tibellus* sp., with $n = 2$, deserves to be ignored). Additional support comes from the *Tetragnatha* spp. data on relative velocity. Given the fact that *D. triton* can also call upon a second aquatic gait, galloping (Suter & Wildman 1999; Fig. 1 inset) when high speed is required, it is reasonable to claim that the data from both of these "specialists" supports the adaptionist rationale for specialized aquatic gaits.

In contrast, the specialized aquatic gaits used rarely among araneids and occasionally among salticids (Table 1) appear to confer no obvious benefit: the absolute and relative velocities achieved by spiders using these rowing gaits are unremarkable when compared to the walking gaits used by *G. rogersi* and *H. ecclesiasticus*. To look more closely

1 Absolute Velocity

D. triton galloping

2 Relative Velocity

walk

row

S1 S2 S3 S4 S5 A1
Salticid or Araneid
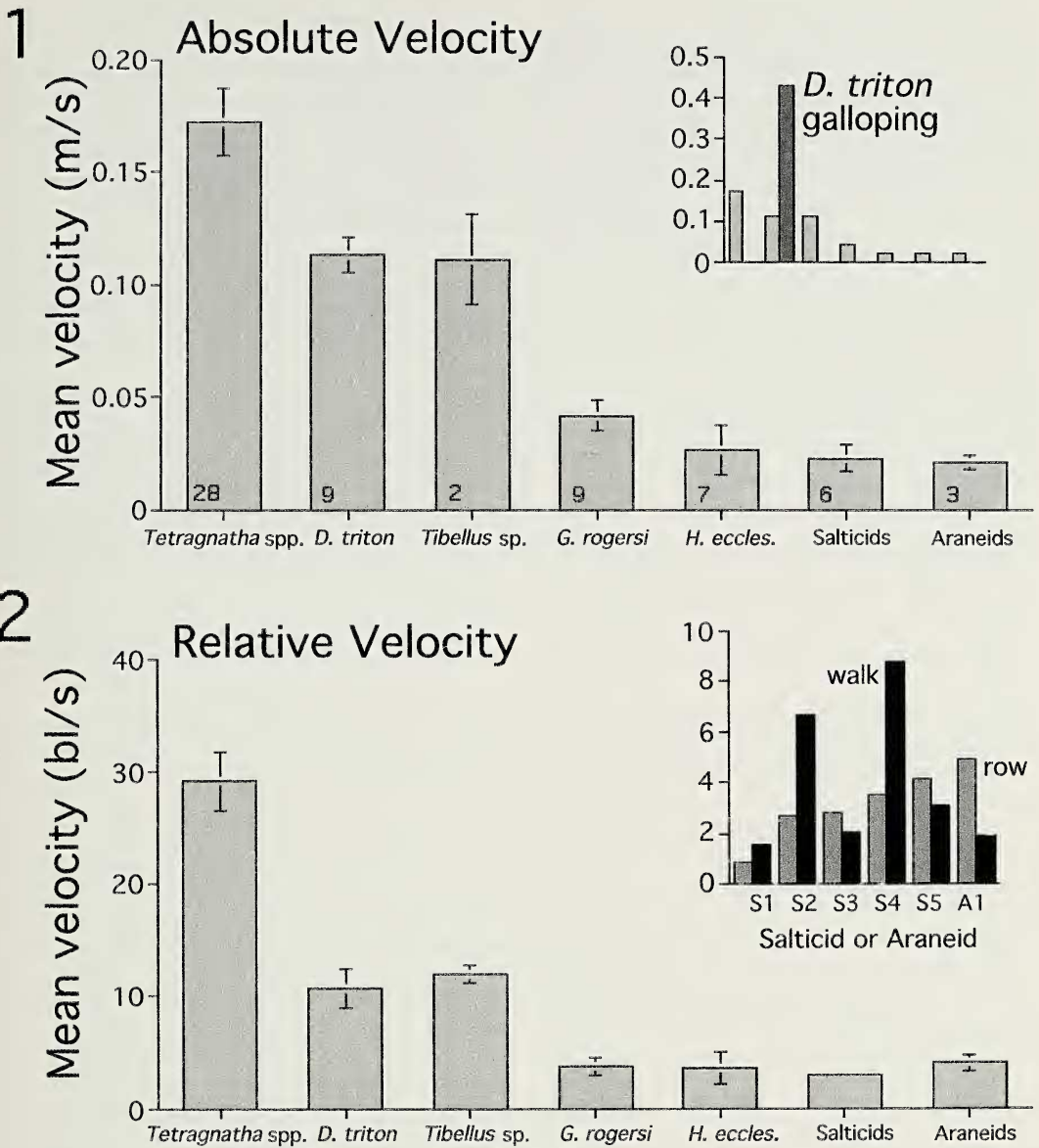
Figures 1–2.—Velocities attained on water by spiders in seven diverse taxa. 1. Absolute velocities: bars represent means ± S.E., with *n* shown at the base of each bar. The bar for *D. triton* represents the rowing gait only; the galloping gait for that species is shown for comparison as the darker bar in the inset. 2. Relative velocities expressed in body lengths per second. For a few individual spiders in the salticid and araneid samples, we also had data on walking (as opposed to a specialized aquatic gait) (inset); here the dark bars represent walking and the lighter bars represent rowing.

at the efficacy of these specialized gaits, we compared the relative velocities achieved by rowing to those achieved by walking in the five salticids and the one araneid in which the individual spiders used both gaits during our test runs (Fig. 2 inset). Even in these within-individual comparisons, the results are equivocal: three of the salticids walked on water

faster than they rowed, and two salticids and the one araneid rowed faster than they walked.

Our data indicate that specialized aquatic gaits occur in at least three families (commonly in Tetragnathidae, but rarely in Salticidae and Araneidae) that are outside of the superfamily Lycosoidea. But only in tetragnathids (along with the pisaurids

which are part of the Lycosoidea) is the propulsion provided by the gait adequate to suggest that its use evolved because of its effectiveness. What remains is a conundrum: we have demonstrated the presence of behaviors in salticids and araneids that appear not to be advantageous to their performers. The rarity of these behaviors is certainly understandable in that context, but their persistence is not. Further investigations may reveal that physiological cost or some other as yet unmeasured parameter explains the presence of these not very effective aquatic gaits.

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